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A new dugong species (*Sirenia*, *Dugongidae*) from the Eocene of Catalonia (NE Iberian Peninsula)*Une nouvelle espèce de dugong (Sirenia, Dugongidae) de l'Éocène de la Catalogne (NE de la péninsule Ibérique)*

Jordi Balaguer, David M. Alba*

Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain

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ABSTRACT

A new stem dugongid species, *Prototherium ausetanum* sp. nov. (Dugongidae, Halitheriinae), is described based on a cranium from the middle Eocene of Mas Vilageliu (Tona, NE Iberian Peninsula). The new species displays a combination of features that enables its distinction from other halitheriines, including *Prototherium veronense* (type species of the genus), *Prototherium? intermedium* (which likely belongs to a different genus), and *Prototherium? montserratense* (here considered a nomen dubium), as well as *Eotheroides* spp. In overall morphology (e.g., dolichocephaly) the new species more closely resembles species previously included in *Prototherium*. However, a cladistic analysis based on craniodental features recovers the new species as the sister taxon of *Eotheroides aegyptiacum* (type species of this genus), further constituting a polytomy with *P. veronense*, *Eotheroides lambdrano* and the remaining Halitheriinae. Our analysis further indicates that *P.? intermedium* is more derived than other species of *Prototherium*, but it does not conclusively resolve the phylogenetic relationships between the included species of *Prototherium* and *Eotheroides*. A deeper taxonomic revision of these two genera would be required in order to better resolve the phylogeny of early dugongids.

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R É S U M É

Une nouvelle espèce basale de dugongidé, *Prototherium ausetanum* sp. nov. (Dugongidae, Halitheriinae) est décrite sur la base d'un crâne de l'Éocène moyen de Mas Vilageliu (Tona, NE de la péninsule Ibérique). La nouvelle espèce montre une combinaison de caractères qui la différencie des autres halitheriins, y compris *Prototherium veronense* (espèce type du genre), *Prototherium? intermedium* (qui appartient probablement à un genre différent), et *Prototherium? montserratense* (ici considéré comme un nomen dubium), ainsi que *Eotheroides* spp. En général, la nouvelle espèce ressemble morphologiquement davantage aux espèces précédemment incluses dans *Prototherium* (par exemple, dolichocéphalie). Cependant, une analyse cladistique basée sur les caractéristiques cranio-dentaires permet de considérer la nouvelle espèce comme le taxon frère d'*Eotheroides aegyptiacum* (espèce type du genre), constituant, en outre, une polytomie avec *P. veronense*, *Eotheroides lambdrano* et les autres Halitheriinae. Notre analyse indique aussi que *P.? intermedium*

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* Corresponding author.

E-mail address: david.alba@icp.cat (D.M. Alba).

est davantage dérivée que les autres espèces de *Prototherium*, mais elle ne résout pas de manière concluante les relations phylogénétiques entre les espèces incluses de *Prototherium* et d'*Eotheroides*. Une révision taxonomique plus approfondie de ces deux genres serait nécessaire, afin de mieux résoudre la phylogénie des premiers dugongidés.

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1. Introduction

Sirenians (manatees and dugongs) are customarily considered to have originated in the Old World, being closely related to the extant Proboscidea and Hyracoidea, as well as to the extinct Desmostylia and Embrithopoda, constituting the Paenungulata clade (Benoit et al., 2013; Domning, 1994; Domning et al., 2010; Gheerbrant, 2009; Gheerbrant et al., 2005; Hautier et al., 2012; Rose, 2006; Uhen, 2007). Until recently, the oldest and most plesiomorphic sirenians had been recorded only from the early or middle Eocene of Jamaica (Domning, 2001b; Savage et al., 1994), but recent finds from the middle Eocene of Senegal (Hautier et al., 2012) and from the early/middle Eocene (Ypresian–Lutetian boundary) of Tunisia (Benoit et al., 2013) further strengthen an African origin of the group. By the Lutetian (middle Eocene), sirenians were already widely recorded in North America as well as the coastal areas of the Tethys (Domning, 2014)—especially along its southeastern (Egypt, Madagascar, India, Pakistan) and northwestern (Spain, Italy, France, Hungary) portions.

The sirenian genus *Prototherium* de Zigno, 1887 (Dugongidae, Halitheriinae), from the middle and late Eocene, displays a European distribution essentially restricted to Spain and Italy (Domning, 1996: 388; Zalmout and Gingerich, 2012: 6, Table 1). Together with the African genera *Eotheroides* Palmer, 1899 and *Eosiren* Andrews, 1902, *Prototherium* is considered a stem dugongid (Domning, 1994), being currently included in the paraphyletic subfamily Halitheriinae. Bizzotto (1983, 2005) suggested that the three above-mentioned genera should be synonymized, thereby resulting in a polytypic and widely-distributed genus *Prototherium* s.l., of high morphological disparity. Eocene dugongids are in need of taxonomic revision (Domning, 1994: 186), but here we tentatively maintain the taxonomic distinction between *Prototherium*, *Eotheroides* and *Eosiren*, as done by most previous authors (Domning, 1994, 1996, 1996; Zalmout and Gingerich, 2012), until a more comprehensive revision is performed (see also the Discussion).

Two species of *Prototherium* are customarily distinguished (Domning, 1996; Zalmout and Gingerich, 2012): *P. veronense*, from the Bartonian (late middle Eocene) of Italy (Domning, 1996; Zalmout and Gingerich, 2012; Zorzini et al., 2012); and *Prototherium? intermedium* Bizzotto, 1983, from the Priabonian (late Eocene) of Italy. Based on currently available phylogenetic analyses, the congeneric status of these species (i.e., the attribution of *P.? intermedium* to *Prototherium*) is doubtful (Domning, 1994: 186). Two additional species were described by Pilleri et al. (1989) from the Bartonian of the NE Iberian Peninsula: *Prototherium solei* Pilleri et al., 1989 and *Prototherium montserratense* Pilleri et al., 1989. The referral

of these species to *Prototherium* is similarly uncertain, and even their taxonomic validity has been disputed by various authors. Thus, Domning (1996, 2014) considered them to be junior subjective synonyms of *P.? intermedium*, whereas Bizzotto (2005) distinguished them merely as subspecies of *P.? intermedium*. For the reasons explained in the Discussion, in this paper we concur with Domning (2014) that *P. solei* is best considered a junior subjective synonym of *P.? intermedium*, whereas *P.? montserratense* is provisionally retained as a nomen dubium (i.e., a nomenclaturally valid taxon of doubtful taxonomic identity).

Here, we describe a new species of *Prototherium*, based on a partial cranium from the site of Mas Vilageliu (see preliminary reports in Balaguer, 2010; Balaguer and Alba, 2012), which was found in 2008 associated with still unprepared postcranial remains. The cranial morphology of the new species allows us to revise the phylogenetic relationships as well as taxonomy of the genus *Prototherium*.

2. Geological background

The site of Mas Vilageliu is located 400 m northwest of the Mas Vilageliu farmhouse and 2 km southwest of the town of Tona (Barcelona, Catalonia, Spain), at the NE end of the Ebro Basin. In this area, Middle to Late Eocene marine sediments crop out along a SW–NE axis from Igualada to Vic (Serra-Kiel et al., 2003). Specifically, the site is located within the Vic-Manelleu Formation, in a layer consisting of the typical, grayish to bluish marls that are Bartonian in age (Pisera and Busquets, 2002).

Among the several invertebrate taxa recovered during the excavations, several poriferans, such as *Guettardiscyphia thiolati* (D'Archiac, 1846), were found growing on the sirenian remains. Previous studies have inferred possible depths greater than 100 m for this sponge (Pisera and Busquets, 2002: 324–325). Sirenians are linked with marine phanerogams (Domning, 2001a: 32; MacFadden et al., 2004: 298), which are absent from such environments within the aphotic zone. This suggests that the sirenian corpse was deposited at such depth after death, being finally buried after a substantial time of low sedimentation, which would have enabled the abundant colonization of its skeleton by *G. thiolati* and other invertebrates.

3. Materials and methods

3.1. Abbreviations

Institutions and fossil collections: CRBMC: Centre de Restauració de Béns Mobles de Catalunya (Valldorèix, Barcelona, Spain); ICP: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain); IPS: acronym of the collections of the ICP; MGSB:

Table 1

Cranial measurements of the holotype of *Prototherium ausetanum* sp. nov. (IPS81881), compared with other *Prototherium* species. Values for *Prototherium veronense* (Pv), the holotype of *Prototherium? intermedium* (Pi) and *Prototherium? "solei"* (Ps) are taken from Pilleri et al. (1989: tables I and VI). Estimated values within parentheses. Measurements for IPS81881 were taken following Zalmout and Gingerich (2012: fig. 8). All measurements in mm, except RD (in degrees, estimated according to the method explained by Velez-Juarbe et al., 2012: fig. 1C).

Tableau 1

Mesures crâniennes chez l'holotype de *Prototherium ausetanum* sp. nov., par rapport aux autres espèces de *Prototherium*. Les valeurs pour *Prototherium veronense* (Pv), l'holotype de *Prototherium? intermedium* (Pi) et *Prototherium? « solei »* sont issues de Pilleri et al. (1989 : tableaux I et VI). Les valeurs estimées sont entre parenthèses. Les mesures pour IPS81881 sont issues de Zalmout et Gingerich (2012 : fig. 8). Toutes les mesures son en mm, sauf pour RD (en degrés, selon le méthode décrit à Velez-Juarbe et al., 2012 : fig. 1C).

	IPS81881	Pv	Ps	Pi
Condylobasal length	> 309	360	(320)	270
Height of jugal below orbit	43	40	27	—
Distance between rear of occipital condyles and anterior end of interfrontal suture	187	220	—	170
Zygomatic breadth	(158)	(140)	(115)	—
Breadth across exoccipitals	(63)	(90)	(80)	—
Distance between top of supraoccipital and ventral sides of occipital condyles	76	(95)	—	—
Length of frontals, level of tips of supraorbital processes to frontoparietal suture	77	127	90	—
Breadth across supraorbital processes	(130)	104	70	85
Breadth across occipital condyles	(47)	(40)	—	—
Breadth of cranium at frontoparietal suture	27	40	27	—
Width of foramen magnum	(19)	(20)	—	—
Length of mesorostral fossa	69	75	68	80
Height of foramen magnum	26	27	—	—
Width of mesorostral fossa	(58)	36	42	31
Maximum height of rostrum	53	68	37	—
Anteroposterior length of zygomatic-orbital bridge of maxilla	> 57	—	—	—
Length of parietals, frontoparietal suture to rear of external occipital protuberance	91	70	70	—
Length of row of tooth alveoli, M1–M3	55	—	—	—
Anteroposterior length of root of zygomatic process of squamosal	—	(45)	37	—
Maximum width between labial edges of left and right alveoli	65	72	64	—
Length of cranial portion of squamosal	—	(68)	62	—
Breadth across sigmoid ridges of squamosals	—	112	—	—
Dorsoventral thickness of zygomatic-orbital bridge	28	—	—	—
Height of posterior part of cranial portion of squamosal	(96)	(85)	67	—
Length of frontals in midline	64	—	—	—
Height of supraoccipital	43	—	—	—
Width of supraoccipital	53	—	—	—
Rostral deflection (RD)	47	50	—	67
Parietal, maximal dorsal breadth	52	38	48	67
Parietal, minimal dorsal breadth	25	34	20	12
Length of nasal	32	70	30	33
Breadth of nasal	24	56	20	34

Museu Geològic del Seminari de Barcelona (Spain); MVT: field acronym for Mas Vilageliu (Tona, Barcelona, Spain).

Anatomical abbreviations: BO: basioccipital; BS: basisphenoid; CL: crista lambdaidea; CT: crista temporalis; EO: exoccipital; FM: foramen magnum; FR: frontal; J: jugal; LAC: lacrimal; MX: maxilla; N: nasal; NPP: nasal process of premaxilla; OC: occipital condyles; PA: parietal; PAL: palatine; PM: premaxilla; PT: pterygoid process; SO: supraoccipital; SQ: squamosal.

3.2. Studied material and comparative sample

This paper is based on the description of the partial skull IPS81881a (field catalog number: MVT10), which was found associated with 45 fragmentary postcranial remains presumably from the same individual. These postcranial remains are currently unprepared because of funding shortage, and therefore cannot be described here. They include: a relatively complete vertebra (MVT27); three partial vertebrae (MVT7, MVT18 and MVT28); partial vertebrae and vertebral fragments (MVT15, MVT29, MVT32, MVT39); partial ribs and rib fragments (MVT1, MVT3–MVT6, MVT12–MVT14, MVT16, MVT17,

MVT20–MVT26, MVT33–MVT36, MVT40–MVT42); and unidentified bone fragments (MVT8, MVT19, MVT30, MVT31, MVT37, MVT38). All these fossil remains are currently housed at the ICP.

Other sirenian specimens examined at the MGSB in the course of this study are the following: type specimens of *P. solei* from Tona (here assigned to *P.? intermedium*), including MGSB48657-2 (holotype, left mandibular ramus with three molars), MGSB48657-1 (paratype, skullcap with supraoccipitals, parietals and frontals) and MGSB48657-4 (paratype, partial maxilla and two associated fragments with three molars and several tooth alveoli); and the holotype of *P.? montserratense* (nomen dubium) from Castellbell i el Vilar (MGSB44892, partial skeleton with cranial and axial elements, still embedded in matrix).

3.3. Anatomical nomenclature

Anatomical nomenclature for the cranium follows Domning (1994), Rose (2006: fig. 2.1) and Zalmout and Gingerich (2012: fig. 8), whereas dental terminology follows Smith and Dodson (2003) and Sorbi et al. (2012: fig. 10A).

3.4. Phylogenetic analysis

The cladistic analysis performed in this paper is based on the data matrix of 69 craniodental characters employed by Vélez-Juarbe and Domning (2014: Supplementary data, Table S1). As in Vélez-Juarbe and Domning (2014), the proboscidean *Phosphatherium escuilliei* Gheerbrant et al., 1996 and the desmostylian *Cornwallius sookensis* (Cornwall, 1922) were employed as outgroups. Besides prorastomid, protosirenid, trichechid and dugongid species already coded by Vélez-Juarbe and Domning (2014), we further coded additional halitheriine dugongids of genera *Eotheroides*, *Eosiren* and *Prototherium*, based on published literature and the observation of fossil material. The newly coded taxa are the following: *Eotheroides lambdrano* Samonds et al., 2009 (based on the original description); *Eosiren libyca* Andrews, 1902 (further based on Andrews, 1906; Domning, 1994); *Eosiren imenti* Domning et al., 1994 (based on the original description); *P. veronense* (based on de Zigno, 1875; Pilleri et al., 1989; Domning, 1994); *P.? intermedium* (including *P. "solei"*; based on Pilleri et al., 1989; Domning, 1994; Bizzotto, 2005; and the material examined by us at the MGSB); and *P. ausetanum* sp. nov. (based on this study). The resulting data matrix is presented in Supplementary data, Table S1. Of the 69 characters included in the data matrix, 7 characters were constant and 12 parsimony non-informative, although they are provided here for the sake of completeness. A cladistic analysis based on maximum parsimony was performed by means of PAUP* 4.0b10 for Unix (Swofford, 2003), with the branch-and-bound option. Following Vélez-Juarbe and Domning (2014), all characters were treated as unordered. Clade stability was assessed by means of Bremer's support indices (which compute the extra steps required in order to collapse a clade in the consensus of near-most-parsimonious trees) as well as with bootstrap analysis (1000 replicates). The Consistency Index excluding uninformative characters (CI), the Retention Index (RI) and the Rescaled Consistency Index (RCI) are reported.

4. Systematic paleontology

Order: Sirenia Illiger, 1811

Family: Dugongidae Gray, 1821

Subfamily: Halitheriinae (Carus, 1868) Abel, 1913

Genus *Prototherium* de Zigno, 1887

Type species: *Halitherium veronense* de Zigno, 1875.

Other included species: *Prototherium? intermedium* Bizzotto, 1983; *Prototherium? montserratense* Pilleri et al., 1989 (nomen dubium).

Prototherium ausetanum sp. nov.

(Figs. 1–4)

Holotype: Partial skull IPS81881a, associated with 45 unprepared fragmentary postcranial elements (not described), and housed at the ICP.

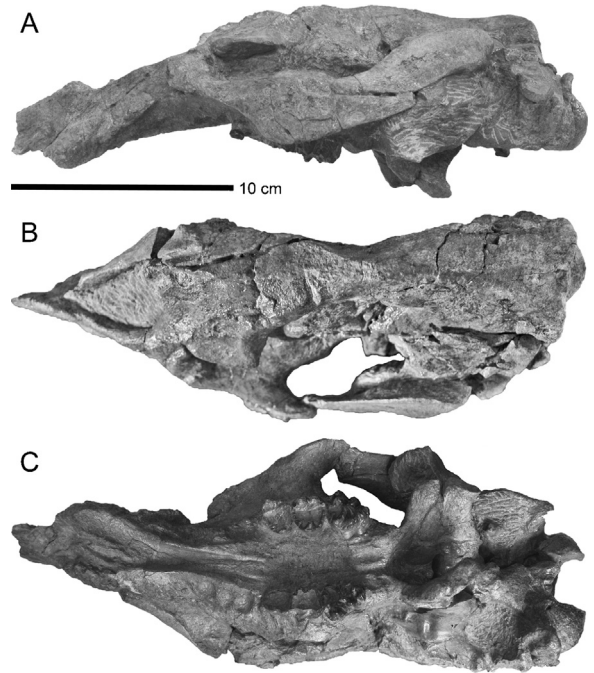


Fig. 1. Holotype IPS81881a of *Prototherium ausetanum* sp. nov., in A. Left lateral. B. Dorsal. C. Basal views.

Fig. 1. Holotype IPS81881a de *Prototherium ausetanum* sp. nov., en vues A. Latérale gauche. B. Dorsale. C. Ventrale.

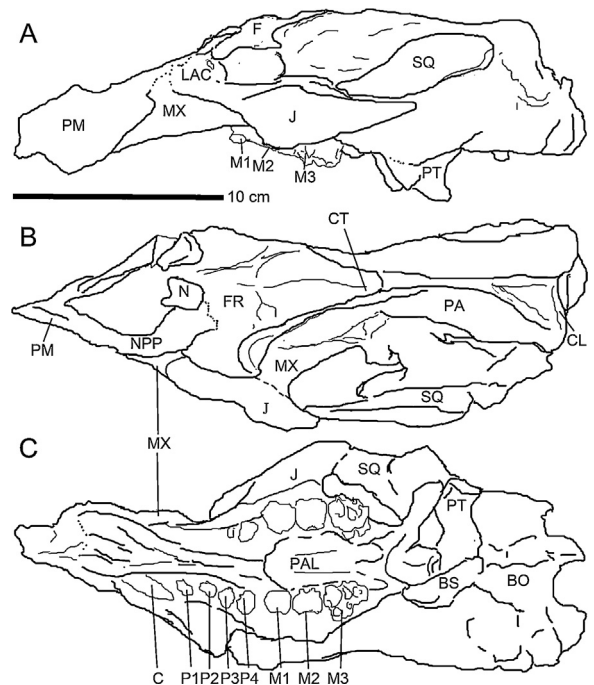


Fig. 2. Line drawings of the holotype IPS81881a of *Prototherium ausetanum* sp. nov., in A. Left lateral. B. Dorsal. C. Basal views.

Fig. 2. Dessins au trait de l'holotype IPS81881a de *Prototherium ausetanum* sp. nov., en vues A. Latérale gauche. B. Dorsale. C. Ventrale.

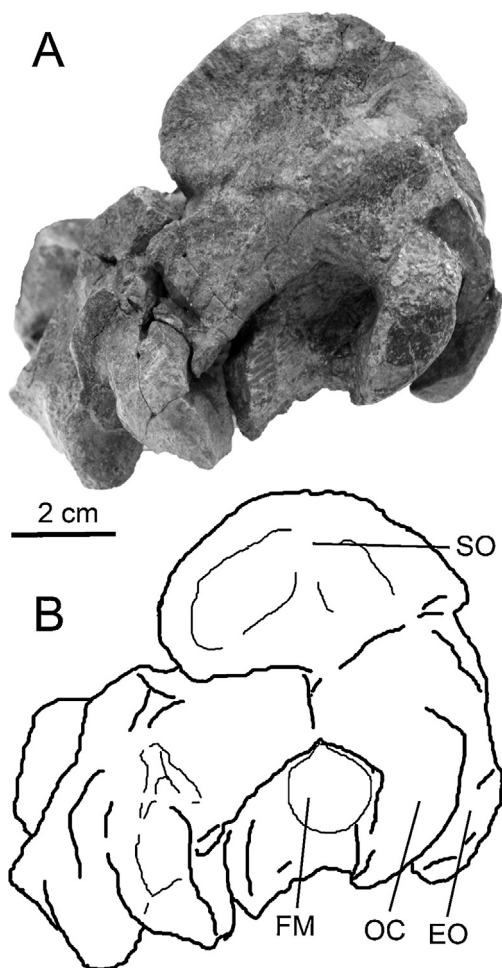


Fig. 3. Holotype IPS81881a of *Prototherium ausetanum* sp. nov., in posterior view. **A.** Photograph. **B.** Line drawing.

Fig. 3. Holotype IPS81881a de *Prototherium ausetanum* sp. nov., en vue postérieure. **A.** Photographie. **B.** Dessin au trait.

Type locality: Mas Vilageliu (Vic-Manlleu Fm., Ebro Basin), dated to the Bartonian (Middle Eocene), within the municipality of Tona (Barcelona, Spain); UTM coordinates: 31 T 434901 E–4632452 N.

Stratigraphic and geographic range: Exclusively known from the type locality.

Etymology: Species name from the Latin, in allusion to the Iberian (pre-Roman) inhabitants of the region (Osona) where the holotype was found.

Diagnosis: Medium-sized species of *Prototherium* with a unique combination of features: rostrum elongated but small relative to cranium; moderate rostral deflection of 47°; lacrimals with foramen; short nasals; supraoccipital trapezoidal in outline, wider ventrally than dorsally; supracondylar fossa of exoccipital present but shallow and located dorsal to condyles; posterior margin of the palatine slightly concave and not incised; M2 rectangular and M3 oval with a postcingulum constituted by two prominent cuspules and enclosing a labially open basin. Other diagnostic features are: long and very mediolaterally compressed cranial vault (with shallow temporal

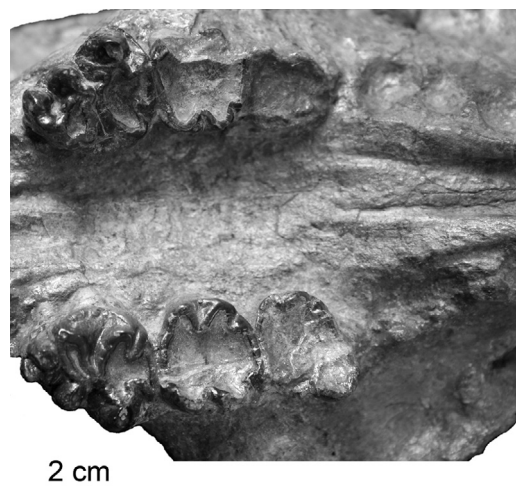


Fig. 4. Detail of the preserved upper check teeth in the holotype IPS81881a of *Prototherium ausetanum* sp. nov., including the right and left P2–P4 alveoli and M1–M3 crowns. Mesial is to the right.

Fig. 4. Détail des dents jugales supérieures chez l'holotype IPS81881a de *Prototherium ausetanum* sp. nov., avec les alvéoles droites et gauches des P2–P4 et les couronnes droites et gauches des M1–M3. À droite, le côté mésial.

fossae); frontals with well-developed supraorbital process and a prominent posterolateral corner; parietals slightly longer than frontals along the sagittal line; zygomatic-orbital bridge of maxilla nearly at the same level as palate.

Differential Diagnosis: The new species differs from all other species of *Prototherium* in the following features: relatively much wider skull, both at the level of the supraorbital process and of the zygomatic arches; trapezoidal supraoccipital wider ventrally than dorsally; well-developed supraorbital process, with a prominent and dorsoventrally-flattened posterolateral corner; parietals slightly longer than frontals; and better-developed M3 postcingulum and accessory cuspules. It further differs from the type species of the genus (*P. veronense*) in the smaller craniodental size; the lower position of the zygomatic-orbital bridge of maxilla; the presence of supracondylar fossa; the non-incised posterior border of palatine; and the shorter nasals. It further differs from *P. ? intermedium* s.l. in the larger cranial size; the lower degree of rostral deflection; the elongated but small rostrum relative to cranium; the more rectangular and narrower cranial vault with mediolaterally shallower temporal fossae; the more rectangular nasals (slightly longer than wide, compared with the holotype); the more rounded foramen magnum; the greater angle between the supraoccipital and the skull roof (compared with the holotype); and the more rectangular M2. Finally, the new species differs from *P. ? montserratense* (nomen dubium) in the more rectangular M2 and the narrower foramen magnum.

In turn, *P. ausetanum* sp. nov. differs from *Eotheroides* spp. in the following features: marked dolichocephaly; shorter nasals; and premaxillary-maxillary suture located behind the premaxillary symphysis instead of below. The new species further differs from *Eotheroides aegyptiacum* (Owen, 1875) in trapezoidal (instead of square) supraoccipital; and from *E. lambdrano*, in the higher degree of

Table 2

Dental measurements (in mm) of the holotype of *Prototherium? ausetanum* sp. nov. (IPS81881a), compared to other *Prototherium* species. Values for *Prototherium veronense* (Pv), the holotype of *Prototherium? intermedium* (Pi), *Prototherium? "solei"* (Ps) and *Prototherium? montserratense* (nomen dubium) (Pm) are taken from Pilleri et al. (1989: tables VII and IX).

Tableau 2

Mesures dentaires (en mm) de l'holotype de *Prototherium ausetanum* sp. nov. (IPS81881a), par rapport aux autres espèces de *Prototherium*. Les valeurs pour *Prototherium veronense* (Pv), l'holotype de *Prototherium? intermedium* (Pi), *Prototherium? « solei »* (Ps) et *Prototherium montserratense* (nomen dubium) (Pm) sont prises à partir de Pilleri et al. (1989 : tableaux VII et IX).

	Pv			Pi			Ps			Pm			IPS81881a					
	M1	M2	M3	M1	M2	M3	M1	M2	M3	M1	M2	M3	Left			Right		
													M1	M2	M3	M1	M2	M3
Mesiodistal length	16	21	23	17	19	—	—	16	17	—	—	—	13.8	16.3	21.6	15.5	16.6	21.4
Anterior breadth	18	21	20	16	16	—	—	16	16	11	17	18.5	—	18.3	19.9	—	—	19.7
Posterior breadth	16	19	16.5	14	13	—	—	12.5	13	—	13.5	15.5	—	18.9	15.4	—	—	14.5

rostral deflection (47° vs. 35°), the presence of lacrimal foramen, and the larger zygomatic-orbital bridge of maxilla.

4.1. Description

The cranium (Figs. 1 and 2) is overall quite complete, although the right side is crushed and only partially preserved (so that several portions, such as the zygomatic arch, are lacking). It is also slightly deformed, with the basal region displaced slightly to the left. The well-preserved left side of the skull (Figs. 1A and 2A) includes both the splanchnocranium and the neurocranium. It probably belongs to a subadult or young adult individual (based on the lightly worn M3 and the unfused basioccipital-basisphenoid suture). Cranial and dental measurements are reported in Tables 1 and 2, respectively. Preserved cranial length is 309 mm; only its rostral-most portion is missing, so that we estimate that its maximum length would not have surpassed 330 mm. Based on a mirror image from the left side, we estimate maximum skull breadth at 158 mm (see also Table 1). Rostral deflection (following Velez-Juarbe et al., 2012: fig. 1C), measured on the left (undeformed) side, is 47°.

Premaxilla: This bone is broken on its anterior-most portion (Figs. 1B and 2B), particularly on the right side, so that the nasal process is completely preserved only on the left side. The rostrum seems to have been long, but small relative to the cranium (c. 3[1] according to our estimate of condylobasal length), with its dorsal surface forming a keel, and the posterodorsal surface forming a boss when viewed laterally (c. 10[1]). The nasal process contacts the frontal bone (c. 9[1]; as is typical of sirenians, see Domning, 1994) and laterally embraces the nasal (c. 6[0]), displaying a sinuous shape when viewed dorsally (Figs. 1B and 2B). The premaxilla is eroded on its ventral side (Figs. 1C and 2C), so that the anterior dentition is missing. The premaxillary-maxillary suture is behind (instead of below) the premaxillary symphysis.

Maxilla: This bone is robust and displays a curved basal contour in lateral view (Figs. 1B and 2B), especially above the molars. The zygomatic-orbital bridge is situated slightly above the alveolar plane (6 mm, c. 11[0]; Figs. 1A and 2A). Due to incomplete preservation, it is not possible to conclusively ascertain whether the zygomatic-orbital bridge is long or shortened (c. 14[?]). The rostral palatal surface of

the maxilla (Figs. 1C and 2C) is broad on its anterior portion, progressively narrowing towards the premolars (c. 23[0]), where it has a groove-like depression (9 mm in width and 42 mm in length) that is deepest at the level of P1–P2. The maxilla slightly widens backwards towards its contact with the palatines, at the mesial level of the M1.

Upper cheek teeth: On the right side, the alveolus of the canine (c. 144[1]; 11.8 mm in mesiodistal length), which preserves tiny dentine fragments, can be discerned. Distally from it, there is a short diastema of 7 mm, followed by the cheek teeth series (c. 151[0]). It includes the empty alveoli of four single-rooted premolars (c. 157[1]), which are interpreted as P1–P4 (c. 145[0], 146[1]) and have a mesiodistal length of 8.4 mm (P1), 7.8 mm (P2), 6.5 mm (P3) and 8.5 mm (P4). They are followed by the molar series (M1 to M3; c. 150[0]), which is preserved on both sides, although the M1 and M2 are very worn and somewhat broken (Fig. 4). The M1 is shorter than the M2, whereas the M3 is longer than the preceding molars (Table 2). The M1 displays a quadrangular occlusal outline, with the protoloph and metaloph apparently of the same width—as far as their worn state allows us to ascertain it. The M2 is more rectangular (broader than long), with the protoloph and the metaloph also similarly wide. Due to its lesser degree of wear (least accentuated on the buccal side), occlusal morphology can be best ascertained on the M3, which clearly displays an oval (distally-tapering) outline and a bunolophodont occlusal pattern. The mesial precingulum displays a large secondary cuspule, which is mostly worn away and connected to the protoloph. The latter is constituted by the worn protocone and paracone (obliterated by wear) as well as the more distinct and protruding, conical paracone. The metaloph, narrower and less protruding than the protoloph, is also tricuspidated, being constituted by hypocone and metacone (partly obliterated and merged with one another due to wear), as well as the more distinct and conical metacone (smaller than the paracone). The central valley between the protoloph and metaloph is narrow but continuous on the right side (where it is only partly interrupted by a short spur originating from the metacone), and more discontinuous on the left side (where the ridge constituted by the hypocone and metacone is linked to the protoloph). A postcingulum originates distally from the hypocone; it curves distolabially and is open labially (well separated from the metacone), being constituted by two secondary cuspules situated on the distolabial corner of the

crown. There is a very narrow labial cingulum around the bases of the paracone and metacone, as well as a wider, but discontinuous and wrinkled lingual cingulum between the protocone and hypocone.

Palatine: The anterior end of the palatine (Figs. 1C and 2C) is situated at the level of the mesial end of the M1 (c. 99[0]). This bone is eroded but complete, and the posterior border of the palatine, slightly deformed, is rounded (c. 97[0]) and situated 13 mm behind the M3. The posterior moiety of the palatine displays a central shallow depression that is 11 mm in width and 20 mm in length. Posteriorly, the palatine constitutes, at both sides, a long process of posterolateral direction that progressively widens to contact anteriorly the pterygoid process.

Nasal: Only the left nasal is preserved (Figs. 1B and 2B), although it is eroded. It is quadrangular and displays a small anterolateral process.

Frontal: The left frontal is complete, whereas the right one is only partially preserved (Figs. 1A, B and 2A, B). It is narrow in its posterior portion, gradually widening anteriorly until constituting the supraorbital process (c. 44[0]). The latter process displays a prominent and dorsoventrally-flattened posterolateral corner (c. 36[0]), and a thickening on the anterolateral corner. A mirror reconstruction based on the left side indicates that the two frontals together would have displayed an overall Y-shape, with an estimated maximum width of 130 mm.

Parietal: Both parietals are preserved, although more fragmentarily on the right side. The braincase is long and narrow, with subparallel lateral sides that broaden only slightly towards the occipital region (Fig. 1B). Dorsally, the two temporal lines shape an elongated and narrow X (Fig. 2B). The sagittal and frontoparietal sutures are practically fused, although their course can be still discerned at several points (so as to provide a reliable reconstruction). The temporal crests are not prominent and moderately curved (type B of Domning, 1988: fig. 3) and closely approach each other (without contacting) along 2.5 cm on their dorsal-most portion. At the intersection of the sagittal suture with the lambdoid crest, there is a shallow, arrowhead-shaped concavity (30 mm long) on the interparietal area (which looks asymmetrical due to distortion). Overall, in lateral view, the cranial vault displays a slightly dorsally convex profile (Figs. 1A and 2A), with the highest point being situated just posterior to the frontal.

Lacrimal: The lacrimal (Figs. 1A and 2A) is fragmentary and little informative. It contacts the jugal bone, forming the anterior border of the orbit. Due to incomplete preservation, it is not possible to ascertain whether the lacrimal contact the premaxilla or not (c. 93[?]). The lacrimal foramen (c. 91[0]), situated anteriorly from the orbit, is oval (7.1 mm long and 4.5 mm wide).

Jugal: The anterior portion of this bone displays a triangular section, with a thin edge on its external portion (c. 88[0]; Figs. 1B and 2B). Due to preservational reasons it is unclear whether the jugal contacts the premaxilla (c. 87[?]). At about the posteroventral edge of the orbit, the jugal becomes dorsoventrally highest (c. 85[0]), with a maximum height of 28 mm behind the orbit (c. 89[0]). The jugal further narrows posteriorly, giving rise to a long and tapering zygomatic process (Figs. 1A and 2A).

Squamosal: The articulation area with the parietal and supraoccipital is very fragmentary and not informative. In dorsal view, the zygomatic process of the squamosal (91 mm long) is straight, and in lateral view its anterior end forms a triangular process above the jugal (c. 81[0]). Medially, the zygomatic process of the squamosal is not swollen (c. 84[0]), while posteriorly it widens dorsoventrally and curves in posterodorsal direction, reaching to a point higher than the dorsal border of the orbital rim and extending to the temporal crest (c. 76[1]). A processus retroversus is present, forming a small bulb moderately inflected in the dorsal moiety of posterior end of the zygomatic process (c. 77[1]; Figs. 1A and 2A).

Occipital region: The supraoccipital (Fig. 3) displays a marked trapezoidal shape, being narrower on the dorsal than on the basal margin (c. 64[1]; maximum width 53 mm), and displaying very rounded contours. The low, nearly inconspicuous external occipital protuberance divides the supraoccipital into two shallow oval concavities. The parietal-supraoccipital angle is 127°. The right exoccipital is quite completely preserved and only slightly deformed, unlike the left one, which is much more fragmentary. A shallow supracondylar fossa is observed dorsal to the condyle (c. 67[1]), with an ellipsoidal shape and a mesioventral to dorsolateral orientation. The dorsolateral border of exoccipital is rounded and seems continuous until the condyle (c. 70[0]). The preserved occipital condyle is 34 mm in height and 20 mm in maximum width. The two exoccipitals contact each other above the foramen magnum along 11 mm (c. 66[0]), and overall have an estimated maximum width of 63 mm. The foramen magnum is rounded with a dorsal peak or indentation, with an estimated maximum width of 19 mm and a height of 26 mm.

Alisphenoid: This bone can only be observed on the right side, where it is however fragmentary. Its lateral surfaces are smooth, and the alisphenoid canal is absent (c. 101[1]).

Pterygoid: It is preserved on both sides, although more clearly observable on the right (Figs. 1A, C and 2A, C). In lateral view, it displays an inverted triangular outline and a deep pterygoid fossa (c. 102[1]). Its distal tip is rounded with a short posteriorly-oriented hamular process (c. 105[1]).

Basioccipital and basisphenoid: The basicranium is very incompletely preserved, because only some fragments of the basioccipital and basisphenoid, which are not informative, can be observed on the right side (Figs. 1C and 2C). These two bones appear not to be completely fused with one another, although their fragmentary preservation precludes an unambiguous assessment.

5. Discussion

5.1. Taxonomic attribution

The cranium IPS81881a displays the diagnostic features of the Dugongidae (see Domning, 1994), such as the lack of the alisphenoid canal, an extension of the squamosal up to the temporal crest, a well-developed processus retroversus, and absence or loss of P5. Its attribution to genus *Prototherium* is further justified by its elongate and narrow

cranial shape (Samonds et al., 2009; Zalmout and Gingerich, 2012). Other features proposed by Bizzotto (1983, 2005), such as the presence of seven postcanine teeth (i.e., presence of four permanent premolars and three molars in adults) and a longer M3 compared to the preceding upper molars, are also present in the new species. However, these features are also displayed by other Eocene sirenians and thus not diagnostic of *Prototherium*. In turn, the presence of an angular process in the posterior edge of the mandible, previously considered diagnostic of *Prototherium* (de Zigno, 1887) but in fact absent from *P.?* *intermedium* s.l. (Bizzotto, 1983, 2005; Pilleri et al., 1989), cannot be ascertained in IPS81881a (which lacks the mandible). Similarly, other cranial features previously considered diagnostic of *Prototherium*, such as a zygomatic–orbital bridge higher than the palate or the length of the nasals roughly one-third of total skull length (Sickenberg, 1934), are not reliable because they are too variable among species currently assigned to this genus (Bizzotto, 1983, 2005; Pilleri et al., 1989) and doubtful in its use.

An attribution of IPS81881a to genus *Prototherium* is further confirmed by the fact that the new species differs from other Eocene dugongid genera in several respects. Thus, compared to the monotypic genus *Sirenavus* Kretzoi, 1941, IPS81881a differs by displaying shorter nasals, and a rectangular (instead of ellipsoidal) cranial vault in dorsal view (see Kordos, 2002; Kretzoi, 1941: fig. 1b). In turn, IPS81881a differs from the scarce material of *Anisosiren* Kordos, 1979 in the smaller upper molars and the less lophodont occlusal pattern of the cheek teeth (Kordos, 1979: 323). It differs from species of *Eosiren* Andrews, 1902 by the shallow instead of deep supracondylar fossa and the shorter (not elongated) M1 and M2 (Zalmout and Gingerich, 2012). An attribution of IPS81881a to *Halitherium taulannense* Sagne, 2001 can be discounted based on the lesser rostral deflection, lack of marked temporal crests and the anterior margin of the palatine not extending to the mesial level of the M1. Finally, the described specimen differs from species currently assigned to genus *Eotheroides* (see Samonds et al., 2009) in the shorter nasals of the former as well as in the position of the premaxillary–maxillary suture (located behind the premaxillary symphysis in the new species, instead of below as in *Eotheroides*). However, the new species shares with *E. aegyptiacum* (type species of the genus) several features that are lacking in other species of *Prototherium*, such as the slightly concave posterior border of the palatine (more incised in *P. veronense* and *P.?* *intermedium*) or the shallow supracondylar fossa of exoccipital (absent in *P. veronense*). In spite of these similarities with *Eotheroides*, an ascription of the new species to this genus instead of *Prototherium* does not seem advisable in the light of the differences with *Eotheroides* noted above, at least according to how these genera are currently conceived.

IPS81881a further resembles other species of *Prototherium* by not retaining the DP5 after the eruption of the upper molars (resulting in an adult dental formula with seven instead of eight postcanine teeth), although the condition of several species of *Prototherium* in this regard has proven controversial. The presence of a P5 has been clearly documented in Prorastomidae and Protosirenidae

(Domning, 2001b; Domning and Gingerich, 1994; Domning et al., 1982; Savage et al., 1994). Among Eocene dugongids, the retention of the DP5 (without substitution by the P5) is quite frequent, being documented in *Eotheroides* (Abel, 1913; Samonds et al., 2009; Zalmout and Gingerich, 2012), *Eosiren* (Andrews, 1902; Domning et al., 1994), *Halitherium taulannense* (Sagne, 2001) and probably *Sirenavus* (Kordos, 2002). In contrast, the lack of DP5 in adults is unusual among Eocene sirenians. The latter condition is displayed by some individuals of *Eotheroides aegyptiacum* described by Abel (1913: 352) and, according to Bizzotto (2005), all the species of *Prototherium* would similarly lack a DP5 in adults. Regarding the type species of the genus, however, Sickenberg (1934) favored the retention of a DP5, based on the presence of an empty space between the inferred P3–P4 and M1–M3 preserved series, but Bizzotto (2005) questioned this interpretation and concluded that *P. veronense* would also lack a DP5. Pilleri et al. (1989), in turn, proposed a dental formula with eight postcanine teeth (retaining the P5 in adults) for *P. solei*, based on their reconstruction of the maxilla. However, our inspection of the paratype MGSB48657-4 indicates that the preserved alveoli cannot be reliably assigned to incisors, canines or single-rooted premolars and that a diastema is displayed mesially from the molars. As such, we consider more likely that this nominal taxon does not differ from other specimens of *P.?* *intermedium* in this regard, thereby supporting the contention that they are best synonymized. At present, however, it is uncertain whether the apparent lack of DP5 in adult specimens of *Prototherium* spp. (including the holotype of the new species described here) has any taxonomic value, being alternatively interpretable as an ontogenetic change with no phylogenetic significance.

The description of a new species, *Prototherium ausetanum* sp. nov., for IPS81881a is justified by the fact that the described holotype cranium differs in various respects from all other species currently included (even if tentatively) in the genus *Prototherium*. The holotype of the new species, based on condylobasal length, is slightly smaller (9%) than *P. veronense* and larger (22%) than *P.?* *intermedium* (on the basis of adult specimens with erupted but not very worn M3; see Fig. 5 for further details). It also displays a relatively wider skull than these taxa (both at the level of the supraorbital process and of the zygomatic arches; Table 1) and a slightly concave posterior edge of the palatine (more incised in *P. veronense*, although not observable in *P.?* *intermedium*). *Prototherium ausetanum* sp. nov. also retains a lacrimal foramen, although this feature cannot be ascertained in other species of the genus (Domning, 1994). The presence of a supracondylar fossa further distinguishes the new species from *P. veronense* (Domning, 1994). Finally, *P. ausetanum* sp. nov. further differs from all other species of *Prototherium* in the occlusal morphology of the M3, which distally displays a postcingulum with two cuspsules that encloses a labially open valley. This morphology is not present in other species of *Prototherium*, which merely display a small cuspsule distally from the metaloph forming the postcingulum (Bizzotto, 1983; Pilleri et al., 1989; de Zigno, 1875).

Compared to other species of *Prototherium*, the cranial vault of IPS81881a (Fig. 5B) displays a rectangular

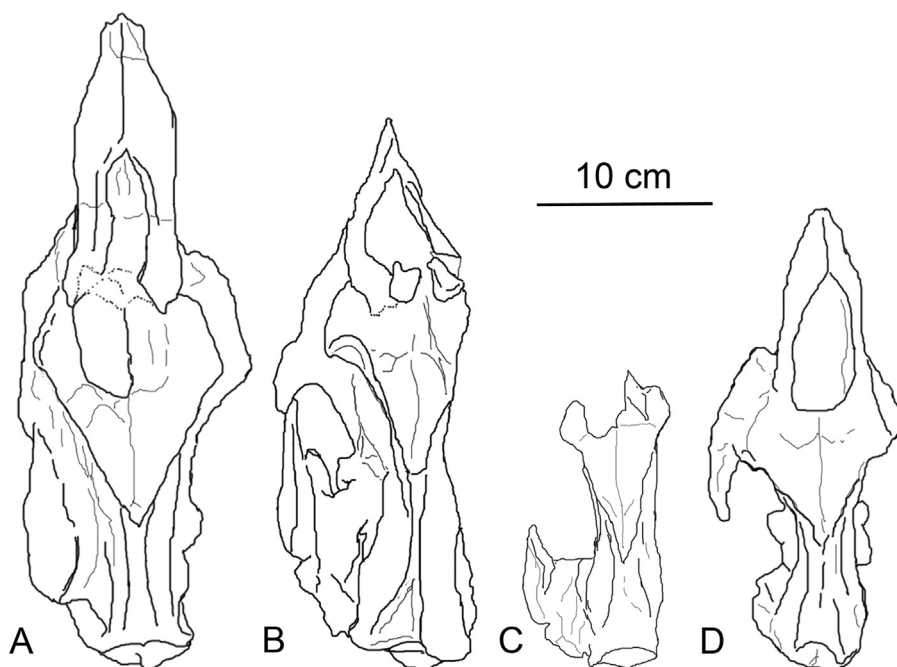


Fig. 5. Dorsal cranial profile of *Prototherium ausetanum* sp. nov., compared with those of other species of the same genus. **A.** *P. veronense* MGP10 (holotype; redrawn from de Zigno, 1875: pl. 18 fig. 1). **B.** *P. ausetanum* sp. nov. IPS81881a (holotype). **C.** *P.?* *intermedium* MGSB48657-1 (paratype of *P. solei*, drawn from the original specimen). **D.** *P.?* *intermedium* 28997 (topotype, redrawn from Bizzotto, 2005: pl. 2B).

Fig. 5. Profil crânien dorsal de *Prototherium ausetanum* sp. nov., par rapport aux autres espèces du genre. **A.** *P. veronense* MGP10 (holotype; redessiné à partir de Zigno, 1875 : pl. 18 fig. 1). **B.** *P. ausetanum* sp. nov. IPS81881a (holotype). **C.** *P.?* *intermedium* MGSB48657-1 (paratype de *P. solei*, dessiné à partir du spécimen original). **D.** *P.?* *intermedium* 28997 (topotype, redessiné à partir de Bizzotto, 2005 : pl. 2B).

shape with the two temporal lines shaping an elongated and narrow X, thus more closely resembling the condition of *P. veronense* (Fig. 5A; de Zigno, 1875). In this regard, the new species differs from *P.?* *intermedium* (Fig. 5D), which displays protruding temporal crests that result in a marked depression in between, as well as a marked widening on the posterior arms of the X (Bizzotto, 2005: pl. 2B). However, it should be taken into account that cranial vault shape is quite variable among sirenians, so that the above-mentioned differences can be even observed among specimens of a single species (e.g., Domning, 1988) and, as such, they have little taxonomic value. *Prototherium ausetanum* sp. nov., in any case, also more closely resembles *P. veronense* in displaying a moderate degree of rostral deflection (47° for the new species and 50° for *P. veronense*, whereas *P.?* *intermedium* shows a more marked deflection of 67°), an elongated but small rostrum relative to cranium (being enlarged in *P.?* *intermedium*), as well as a trapezoid supraoccipital (instead of quadrangular as in *P.?* *intermedium*; Pilleri et al., 1989: pl. XVI; Bizzotto, 2005: fig. 4A). The rounded foramen magnum of *P. ausetanum* sp. nov. further differs from that of *P.?* *intermedium* (which is ellipsoidal; Bizzotto, 2005: fig. 4B), but it cannot be confidently compared with that of *P. veronense* due to distortion in the latter. In contrast, *P. ausetanum* sp. nov. more closely resembles *P.?* *intermedium* in the short nasals, contrasting with the longer condition displayed by those of *P. veronense* (presumably representing the plesiomorphic condition; Domning, 1994), as well as in the position of the zygomatic-orbital bridge (at about the level of the

palate, instead of higher above the latter as in *P. veronense*; Domning, 1994).

With regard to the two nominal species previously described by Pilleri et al. (1989) from Eocene remains of two Catalan localities, due to preservational reasons, detailed comparisons are only feasible with *P. solei*. This taxon, originally described as a distinct species of *Prototherium* from the Bartonian of Tona, was subsequently synonymized with *P.?* *intermedium* by Domning (1996, 2014), whereas Bizzotto (2005) merely distinguished these taxa at the subspecies rank. Given that *P. solei* only differs from the nominotypical subspecies in size and a few other morphologic features of little taxonomic value (Bizzotto, 2005), with no differences in the character codings for the matrix employed in this paper (at least, regarding those features preserved in both nominal taxa), here we concur with Domning (2014) that *P. solei* is best considered a junior subjective synonym of *P.?* *intermedium*, in spite of the age differences between their respective type localities. Given that both *P. ausetanum* and *P. "solei"* come from the same area and are older (from the Bartonian) than the type locality of *P.?* *intermedium* (from the Priabonian), the differences between the new species and specimens of *P.?* *intermedium* previously attributed to *P. solei* deserve particular attention. Thus, in spite of a similar overall cranial size, the holotype of *P. ausetanum* sp. nov. differs from *P. "solei"* (paratypes MGSB48657-1 and MGSB48657-4) in several cranial measurements (Table 1), with the former displaying much longer parietals as well as a much wider skull (both at the level of the supraorbital processes and at that of

which differ from the more plesiomorphic dugongids *Prototherium* and *Eotheroides* in the larger rostrum relative to the cranium. In other words, our analysis does not resolve the relationships between the species of the basal dugongid genera *Prototherium* and *Eotheroides*, except for the fact that *P.?* *intermedium* occupies a more derived position (as the sister taxon of *Halitherium taulannense*). This suggests that *P.?* *intermedium* should be removed from genus *Prototherium*, although we refrain from providing an alternate genus ascription until the genus *Halitherium*, which apparently is not monophyletic (Vélez-Juarbe and Domning, 2014; Voss, 2013), is revised. In fact, the results of our analysis further highlight that the more plesiomorphic genera *Prototherium* and *Eotheroides* are also in need of revision. A more comprehensive analysis, including additional species of *Eotheroides*, would be required to more confidently resolve the phylogenetic relationships between these taxa. In the meantime, we prefer to include the newly described species into *Prototherium*, based on the morphological features discussed in the preceding section.

6. Conclusions

A new sirenian species, *Prototherium ausetanum* sp. nov. (Dugongidae, Halitheriinae), is described based on a well-preserved cranium from the Eocene of Mas Vilageliu (Tona, NE Iberian Peninsula). The new species can be distinguished from other species of *Prototherium* in cranial as well as dental features, including not only *Prototherium veronense* (the type species of the genus), but also *Prototherium?* *intermedium* (provisionally retained with doubts in the same genus) and *Prototherium?* *montseratense* (of uncertain taxonomic validity, and hence considered a nomen dubium). The new species thus differs from other sirenian remains from the area of Tona, which are referable instead to *P.?* *intermedium*. A cladistic analysis based on craniodental features does not recover the monophyly of genus *Prototherium*, by grouping the new species with *Eotheroides aegyptiacum*, whereas *P.?* *intermedium* clusters with more derived halitheriines. In fact, the results of our phylogenetic analysis do not recover the monophyly of any other Eocene genera (*Eotheroides*, *Eosiren* and *Halitherium*), merely suggesting that *Eotheroides* and *Prototherium* (with the exclusion of *P.?* *intermedium*) are more basal than the remaining dugongids included in our study. In light of these results, we attribute the new species to *Prototherium* based on several morphological features (such as dolichocephaly) classically employed to distinguish this genus from *Eotheroides*, while stressing at the same time that these two genera (and *Halitherium* as well) are in need of in-depth revision. However, the data first reported here for various of these Eocene taxa should be useful, once integrated with those for other genera such as *Halitherium* (Voss, 2013, 2014), for providing a more comprehensive phylogenetic and systematic revision of the Eocene Dugongidae in the future.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2015.10.002>.

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